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THE MANY FACES OF FEAR: A SYNTHESIS OF METHODOLOGICAL VARIATION IN CHARACTERIZING PREDATION RISK FROM CARNIVORES

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ABSTRACT

1. Predators affect prey by killing them directly (lethal effects) and by inducing costly antipredator behaviors in living prey (risk effects). Recent research in carnivore-ungulate systems has shown how risk effects can strongly influence prey populations and cascade through trophic systems. A crucial prerequisite for assessing risk effects is characterizing the spatiotemporal variation in predation risk.

2. Carnivore-ungulate risk effects research has experienced rapid growth. However, preliminary assessments of the resultant literature suggests that researchers characterize predation risk using a diverse variety of techniques. This methodological variation complicates inference about risk effects and confounds comparability between studies due to an evident lack of clear benchmarks.

3. We couple an extensive literature survey with a hierarchical framework, developed from established theory, to quantify the methodological variation in characterizing risk from carnivores.

4. We detected substantial variation in methods characterizing risk from carnivores, with 243 metrics of risk from 141 studies falling into at least 13 distinct subcategories within 3 broader categories. Most studies characterized predation risk in relatively simplistic terms, often using a single metric to represent risk. We also documented a strong focus in the literature on a specific trophic interaction (wolf *Canis lupus* – elk *Cervus elaphus*).

5. Our synthesis suggests that the gaps in our understanding of carnivore-ungulate risk effects are due, at least in part, to the methodological variation in characterizing predation risk and an overarching research focus on wolf-elk systems. We provide recommendations to guide future work, including calls to evaluate risk effects related to a greater diversity of carnivore species

and for studies to strategically characterize risk so that key, unifying hypotheses regarding carnivore-ungulate risk effects can be adequately tested.

Keywords: antipredator behavior; carnivore; landscape of fear; nonconsumptive effects; nonlethal effects; predator-prey interaction; predation risk; risk effects; study design; ungulate

INTRODUCTION

Predation fundamentally shapes species interactions and drives numerous aspects of community, population, and ecosystem ecology (Lima 1998a; Werner & Peacor 2003; Barbosa & Castellanos 2005). Predators' influence on prey can be broadly divided into two categories. First, predators kill prey: the *lethal effect* (also called the *density* or *consumptive effect*; Werner and Peacor 2003, Preisser *et al*. 2005). Second, predators influence plastic behavioral, physiological, or morphological traits of prey seeking to avoid predation: the *risk effect* (also called the *trait, non-consumptive*, or *nonlethal effect*; Lima 1998a, Werner and Peacor 2003, Creel and Christianson 2008, Heithaus *et al*. 2008). Whereas the foundation of predator-prey research was established with a focus on lethal effects (cf. Holling 1959), more recent research, encompassing a diverse range of taxa and systems, has revealed the central importance of risk effects (Lima 1998a; b; Werner & Peacor 2003; Creel & Christianson 2008; Cresswell 2008; Heithaus *et al.* 2008). Risk effects research has shown how the threat of risk can strongly influence prey distribution, demography, and behavior (Lima 1998a; Werner & Peacor 2003; Heithaus *et al.* 2008) and regulate the strength of top-down and bottom-up forces in community interactions (Laundré *et al.* 2014; Ford & Goheen 2015).

Although risk effects have been relatively well-documented in smaller systems (e.g., aquatic invertebrate food webs; Werner and Peacor 2003), they have only recently been assessed in systems with wide-ranging predators and highly mobile prey (e.g., carnivore-ungulate systems; cf. Ford and Goheen 2015). For example, of the many hundreds of studies included in reviews covering risk effects published in the last two decades (e.g., Lima 1998b, Preisser *et al*. 2005, 2007, Paterson *et al*. 2013, Weissburg *et al*. 2014), only a minority were conducted in carnivore-ungulate systems. Furthermore, not one of the 453 studies reviewed by Preisser *et al*. (2005, 2007) was carried out in a carnivore-ungulate system (cf. Weissburg *et al*. 2014). This lack of studies is likely due to a combination of the ethical challenges associated with experimentation on large, sentient animals and the logistical challenges related to vast spatial scales and sample size constraints associated with large carnivores (Estes 1995).

Nevertheless, research on carnivore-ungulate risk effects has increased dramatically in the past decade (Fig. 1) and the "landscape of fear" model of carnivore-ungulate interactions proposed by Laundré *et al*. (2001) has become an influential concept. Recent syntheses have collated this work into a more cohesive theory. For example, Creel and Christianson (2008) explored the fitness costs of risk effects and the synergistic contributions of lethal and risk effects to ungulate prey population dynamics, while Creel (2011) drew upon carnivore-ungulate examples to form general predictive hypotheses regarding how characteristics of prey, predators, and the environment might modulate risk effects. Yet more recent work calls for increased experimental manipulation to reveal carnivores' mechanistic role in triggering trophic cascades (Ford & Goheen 2015).

However, the recent proliferation of carnivore-ungulate risk effects research has created a challenge: variation in how "risk" is characterized and measured, which in turn affects the interpretation of studies and the comparisons made among them. Variation in how risk is characterized in carnivore-ungulate systems is exemplified by research on gray wolves (*Canis* *lupus*) and their primary prey, elk (*Cervus elaphus*), throughout North America. In these studies, predation risk from wolves has been characterized in numerous ways (cf. Moll *et al.* 2016b), including broadly delineated areas of wolf-pack presence and absence (Laundré, Hernández & Altendorf 2001; Christianson & Creel 2014), measures of habitat characteristics associated with increased risk of wolf predation (e.g., habitat openness; Ripple and Beschta 2003), estimated wolf-elk encounter and predation rates (Hebblewhite & Pletscher 2002), wolf-elk population ratios (Creel *et al.* 2007), the daily presence or absence of wolves in a river drainage (Creel *et al.* 2005; Winnie Jr & Creel 2007; Christianson & Creel 2010), and the instantaneous distance between elk and wolves at a given time (Creel, Winnie & Christianson 2013; Middleton *et al.* 2013). Such variability has important implications for inference and comparability among studies (Creel *et al.* 2013) and has been evoked by several research groups in debates over the presence, magnitude, and scope of wolf-elk risk effects in Yellowstone National Park, U.S.A (e.g., see Kauffman *et al*. 2010, 2013, Winnie Jr. 2012, 2014, Beschta and Ripple 2013, Creel *et al*. 2013, Middleton *et al*. 2013, Beschta *et al*. 2014). Methodological variation is not unique to Yellowstone; these studies simply provide a magnifying lens by which to examine a widespread tendency in the carnivore-ungulate risk effects literature to define, measure, model, and interpret risk from carnivores using a variety of techniques. Here, we explore the depth of this variability with the following four objectives: 1) synthesize the ways in which predation risk has been characterized in the carnivore-ungulate risk effects literature, 2) quantify the variation exhibited, 3) discuss the implications of this variation on inference and comparability between studies, and 4) provide research recommendations.

METHODS

Survey of carnivore-ungulate risk effects literature

In May of 2016 we used the Web of Science to survey the carnivore-ungulate risk effects literature using the following search terms: (carnivore AND ungulate) AND ("predation risk" OR "landscape of fear" OR "risk effects" OR trait-mediated OR nonlethal OR non-lethal OR nonconsumptive OR behaviorally-mediated). Next, we eliminated unrelated studies, those that did not measure risk effects or modeled predation risk as a response variable (i.e., studies evaluating the effectiveness of anti-predator behaviors for increasing prey survival), and those for which *Homo sapiens* were the only predator considered. We then categorized all predation risk metrics such that each fell into one of the three main categories and one of the 13 subcategories described in the framework below (see Appendices A and B for a full list of studies and metrics). We also included an "other" subcategory within each of the main categories for rarely-used or unique metrics.

A framework for predation risk metrics

Our framework relied upon categorizing *metrics* of predation risk, where a metric is any measurement or variable referencing the risk of predation from carnivores. Metrics could be stand-alone variables (e.g., the presence/absence of a carnivore at a site) or model outputs such as the probability of carnivore occurrence. We developed this framework as a two-level hierarchy, described in detail below. At the first level, we divided metrics into one of three *categories*, including *risky places* and *risky times* categories that respectively captured long- and short-term risk from carnivores, and a *habitat characteristics* category that captured metrics that indexed risk via landscape features. At the second level, we sorted metrics into *subcategories* of metrics that were methodologically similar (Table 1, Fig. 2).

We developed our framework as a useful means to synthesize the variation in carnivore risk metrics rather than as a prescriptive template for all risk effects research. Accordingly, we have avoided overly-rigid terms and definitions, especially given that they can stifle rather than stimulate progress in emerging research areas (Hodges 2008). Therefore, the categories and subcategories described below represent a trade-off of internal consistency (i.e., all metrics within a category or subcategory similar) and flexibility (i.e., allowing variation within a given category or subcategory).

Categories of risk

We constructed three categories of risk around concepts underlying several basic hypotheses regarding predation risk and antipredator behavior. In an early and influential review on risk effects, Lima and Dill (1990) decomposed risk into three core components: 1) predator-prey encounters, 2) death given an encounter, and 3) time spent vulnerable to encounter (cf. Holling 1959), represented in the following equation:

$$P(\text{death}) = 1 - \exp(-\alpha d T), \quad (1)$$

where P(death) is the probability of being killed, α is the predator-prey encounter rate, d is the probability of death given an encounter, and T is time spent vulnerable to encounter. Subsequently, Lima & Bednekoff (1999) proposed that a fourth component of risk, its temporal variability, is crucial to understanding antipredator behavior in prey. They formalized this concept in the *risk allocation hypothesis*, which states that the level of antipredator behavior at a given time is contingent upon the temporal sequence of risk in which it is embedded. That is, antipredator behavior depends on both the immediate and the background level of predation risk. On this view, prey are expected to exhibit the strongest antipredator behavior during brief pulses of risk that occur within low background risk situations (e.g., encountering rare but dangerous predators) and the weakest antipredator behaviors during pulses of safety that occur within the context of high background risk (e.g., predators locally absent in an area with high predator densities; see Fig 3 in Lima and Bednekoff 1999). Creel et al. (2008) outlined two alternatives to the risk allocation hypothesis. The *risky places hypothesis* states that antipredator behavior varies only in relation to long-term background risk, irrespective of pulses of risk or safety whereas the *risky times hypothesis* articulates that antipredator behavior varies only in relation to brief pulses of predation risk, regardless of background risk.

We used the concepts of background risk and pulses of risk to separate predation risk metrics into two broad categories: long-term metrics representative of "risky places" and short-term metrics representative of "risky times". The key aspect that differentiating these categories is the time period over which a metric characterized risk. For example, in a risky places approach, data might be collected daily (e.g., GPS locations of a carnivore) but subsequently averaged over a broader time frame (e.g., an annual home range). In contrast, risky times metrics link ungulate behavior to carnivore predation risk at much finer scales, ranging from instantaneous (e.g., direct observations of carnivore hunts; Lingle 2002) to daily periods (e.g. daily response to simulated carnivore cues; Kuijper *et al*. 2014).

The risky places/risky times dichotomy is a useful way to categorize metrics of carnivore space use or behavior. However, risk is also commonly represented using habitat characteristics. These characteristics are either hypothesized to correlate with risk or interact with carnivore space use or behavior to modulate risk. For example, edge habitat tends to be associated with higher risk from ambush carnivores (e.g., African lions *Panthera leo*; Prins and Iason 1989, Moll *et al*. 2016a) and therefore might approximate risk from particular carnivores. Other habitat features interact with carnivore presence. For example, fallen logs obstruct ungulate escape and might increase mortality risk during an attack, making risky times riskier (Kuijper *et al*. 2013, 2015). Thus, rather than subsume habitat characteristics within the risky places/risky times dichotomy, we delineated habitat as its own category that has relevance to either risky places metrics, risky times metrics, or both, depending on the context (Fig. 2). This category is further justified by the common practice across taxa to use habitat characteristics as stand-alone metrics of risk without explicit measurements from actual predators (Verdolin 2006; Appendix A).

Subcategories of risk

The breadth of the categories described above necessitated a second step to form groups of similar metrics within each category. We therefore identified 13 subcategories of risk metrics (described in Table 1; Fig. 2; Fig. 3). We defined subcategories such that the metrics within each had 1) relatively similar methodologies and 2) the same general expected relationship to two basic components of risk contained in Eq. 1: encounter rate (α) and probability of death given an encounter (d; see Fig. 3). We determined the expected relationships between a given subcategory and α and d qualitatively based upon the hypotheses, assumptions, and results of studies in our literature survey as well as other relevant literature and our own experience in carnivore-ungulate systems (see Appendix C; Fig. 3). For example, *carnivore density* and *probabilistic carnivore occurrence* metrics (Table 1) tend to vary positively with encounter rates (e.g., Ford *et al.* 2014), with little or no relation to the probability of death given an encounter (Fig. 3b,c). Other metrics, such as those in the *escape impediments* subcategory, are more related to the probability of death given an encounter than encounter rates (e.g., Kuijper *et al.* 2015; Fig. 3k). Other subcategories' metrics are expected to vary with both parameters. For example, areas of high predation risk predicted by models of *probabilistic kill occurrence* are often locations where both encounter rate and probability of death given an encounter are high (e.g., Hebblewhite & Merrill 2007; Fig. 3d). Similarly, *distance to the nearest carnivore* (e.g., Middleton *et al.* 2013) and *protective* *cover* (e.g., Bowyer *et al.* 1999) metrics tend to have a negative relationship with both encounter rate and death given encounter (Fig. 3f,j). We note for clarity that the relationships illustrated in Fig. 3 are intended to highlight how the subcategories of metrics relate to unique aspects of risk and stimulate future research into their true functional forms; they are not average effect sizes of the studies included in our survey.

Therefore, we hierarchically categorized risk metrics in the two-step framework described above such that each belongs to one of three broad categories and one of 13 relatively homogeneous subcategories (Fig. 2, Fig. 3).

RESULTS

Our literature survey returned 275 studies referencing predation risk in carnivore-ungulate systems. After removing inapplicable studies (see Methods), we retained 141 studies that used 243 distinct metrics of predation risk.

Few studies (N = 16; 11.3%) examined predation risk from > 1 carnivore species. Species from the family *Canidae* were the most common carnivores assessed (N = 100; 70.9% of the studies). Gray wolves were a study species in 85 studies (60.3%), 77 of which considered them the sole source of risk (i.e., predation risk from co-occurring carnivore species unmeasured). Species from the family *Felidae* were the next most commonly-studied family of carnivores (N = 32; 22.7%), with a focus on African lions (N = 13 studies). Other carnivores studied included bears (Genus *Ursus*; N = 10), spotted hyena (*Crocuta crocuta*; N = 3), and Tasmanian devil (*Sarcophilus harrisii*; N = 1). In addition, 10 studies indiscriminately assessed risk from multiple carnivores either via habitat characteristics (e.g., visibility) or by comparing areas with multiple carnivores to areas with few or no carnivores (see Appendix A). Our survey returned few or no studies of risk effects for cheetah (*Acinonyx jubatus*; two studies), tiger (*Panthera tiger*; two studies), snow leopard (*Panthera uncia*; no studies), and dhole (*Cuon alpinus*; no studies).

A slight majority of the studies (N = 84; 59.6%) used a single metric to characterize risk, with the remainder of the studies using a mean of 2.8 metrics (SD = 1.6, range 2-10) each. Across all studies, approximately half of the metrics (N = 113; 46.5%) characterized risk in a long-term fashion consistent with the idea of risky places, with the remainder split between risky times (N = 57; 23.5%) and habitat characteristics (N = 73; 30.0%; Table 2). No metric subcategory was dominant, with probabilistic approaches to carnivore occurrence being the most common (N = 37, 15.2%) and observed interactions the least common (N = 5; 2.1%; Table 2).

Considerable variation existed among individual metrics within subcategories. Such variation is illustrated via a detailed look at one of the subcategories, probabilistic carnivore occurrence. Utilization distibutions (UDs) were a commonly-used metric to model probabilistic carnivore occurrence (used in 11 studies), but specific methodologies varied. The timeframes over which UDs were constructed ranged from 30 days (Thaker *et al.* 2011) to 24 months (Moll *et al.* 2016a), with a mean of 8 months (SD = 7.8). Some studies converted UDs into categorical variables (e.g., “high risk” inside the 50% isopleth of a UD; de Azevedo and Murray 2007), whereas others used the continuous UD percentile to quantify risk (e.g., Moll *et al*. 2016a). Yet others used the mean value of the portion of a carnivore’s UD falling within an ungulate’s home range (Nicholson *et al.* 2014). Studies also exhibited variation in the user-defined kernel bandwidths (smoothing parameters) used to generate UDs, with studies using reference (Valeix *et al.* 2009), plug-in (Moll *et al.* 2016a), least-squares cross-validation (Thaker *et al.* 2011), and other methods (Kauffman *et al.* 2010). Bandwidth choices affect UD size and shape, with potential to both over- and undersestimate carnivore occurrence (Gitzen, Millspaugh &

Kernohan 2006). Variation in UD methodology is representative of variation present within most subcategories (Appendix A).

DISCUSSION

General trends

Predator-prey ineractions are multifacted and dynamic and the variation in characterizing risk uncovered by our synthesis is a reflection of that inherent complexity. No subcategory of metrics in our framework was predominant, highlighting substantial variation in the methods used to characterize predation risk among the studies assessed (Table 2). Such variability complicates discussion over the presence and strength of risk effects in ungulates because no benchmark exists for how to characterize predation risk and certain metrics might be more contextually appropriate for a given ungulate response than others (Moll *et al.* 2016b). Moreover, the tendency to use a single metric to characterize risk (Table 2) means that many studies only provide a snapshot into the complicated dynamics of risk and response in carnivore-ungulate systems. This oversimplification becomes problematic when a given studies' results are contingent upon sampling scheme or duration but are interpreted in an absolute or over-generalized manner. Building knowledge of complex predator-prey interactions often requires decomposing risk into its consituent components, examining them in isolation, and then painstakingly piecing the findings back together into a comprehensive theory (Werner & Peacor 2003; Schmitz 2005). The present challenge for carnivore-ungulate risk effects research is to build upon current knowledge efficiently, a point to which we return in the concluding section on research recommendations.

Our results suggest risk effects research in carnivore-ungulate systems is strongly influenced by a single carnivore, the gray wolf, and its primary prey in North America and Europe, elk and red deer respectively. The dominant focus on the gray wolf, coupled with the relative lack of studies on numerous other carnivores, means that despite the recent exponential increase in research effort (Fig. 1), substantial and perhaps dramatic gaps remain in our understanding of risk effects in carnivore-ungulate systems. Given that ambush predators tend to elicit stronger risk effects than active ones (Preisser *et al.* 2007), the general emphasis on actively hunting carnivores (e.g., canids) might translate to an overall underestimation of risk effects in carnivore-ungulate systems. This underestimation is accentuated by the historic focus on lethal effects of predators on prey (Lima 1998a). It is therefore likely that future research will continue to confirm the traditionally overlooked importance of carnivore risk effects in shaping predator-prey interactions, community ecology, and ecosystem dynamics (Lima 1998a; Creel & Christianson 2008).

Many studies in our survey focused on documenting the presence of risk effects rather than their mechanistic underpinnings. For example, nearly 20% of metrics used a carnivore presence/absence approach to relate ungulate behavior to risk (Table 2). Such an approach is fitting for documenting the presence of risk effects but is not well suited to uncover how such effects arise or how their magnitude varies with different levels and/or types of risk. The focus on documentation of a phenomenon is somewhat common in emerging areas of research (Werner & Peacor 2003), yet this approach is probably a suboptimal method for building ecological knowledge when compared to a more mechanistic, hypothesis-driven strategy (Moll *et al.* 2007). In their review of risk effects in aquatic systems, Werner and Peacor (2003) noted, "empirical workers must take more care to focus on the functional relations required in the theory rather than simply documenting the presence of a phenomenon" (pg. 1096). Our results suggests their sentiment can be applied to carnivore-ungulate systems.

Under- and overestimating risk effects

Subcategories of metrics differ in their tendency to under- or overestimate predation risk, which complicates comparisons among studies. Presence/absence metrics, both in the risky places and risky times contexts, tend to underestimate risk because failing to detect a carnivore when truly present is more likely than detecting one when truly absent (Winnie Jr & Creel 2007; Christianson & Creel 2008). Similarly, Creel *et al*. (2013) note that distance to carnivore metrics using GPS-collared individuals are susceptible to underestimating risk because 1) carnivores might be near prey between GPS fixes, resulting in undetected encounters, and 2) encounters between ungulates and uncollared carnivores are undetected in the common situation where only a subset of a carnivore population is fitted with GPS-collars. Together, these three subcategories (risky places and risky times presence/absence and distance to carnivore) constitute nearly a quarter of all metrics in our literature survey (Table 2), once again highlighting the potential for substantial underestimation of risk in current carnivore-ungulate research.

Risk can be overestimated in at least two cases. First, carnivore cues (e.g., scent, scat, or auditory cues) can be simulated in ways that over-represent natural systems. Weissburg *et al*. (2014) suggest such over-representation is common in aquatic studies using chemical cues to study antipredator behavior in invertebrate prey. In carnivore systems, predator cues have been simulated via carnivore urine, feces, feces extract, scent, and audio playbacks (Appendix A). These studies are usually replicated and controlled experiments and as such hold much promise for advancing mechanistic understanding of carnivore-ungulate risk effects (Ford & Goheen 2015), but care should be taken to ensure cues are propagated in biologically realistic manners

(Weissburg *et al*. 2014). Second, studies conducted over short periods (e.g., weeks) have potential to overestimate risk effects if results are considered to be representative of long-term responses. For example, Luttbeg *et al*. (2003) showed a tritrophic cascade mediated via risk effects observed in one portion of a season was a poor representative of overall effects throughout a season. The results of short-term studies, especially experimental manipulations of carnivore presence, should be tested against long-term studies to guard against overestimation of risk and its subsequent relation to trait-mediated trophic cascades (Abrams 2008). A yet better approach is to measure both long-term risk and short-term risk simultaneously, as such studies can test the risk allocation hypothesis against simpler risky places and risky times hypotheses (Creel *et al.* 2008)

Relating metric subcategories to risk at multiple scales

We qualitatively postulated how the various subcategories of risk might relate to the core components of risk (encounters and death given an encounter; Fig. 3), but the functional forms of the relationships depicted therein are largely unstudied and unknown (Cresswell 2008). Nonlinear relationships between both a given metric and predation risk, and risk and a particular risk effect (e.g., increased vigilance), are likely. For example, given the non-random space use of both carnivores and ungulates, a linear relationship between carnivore density and the encounter rate (Fig. 2b) is doubtful (Whittington *et al.* 2011). Under the risk equation provided above (Eq. 1, Lima and Dill 1990), metrics that simultaneously capture changes in both encounter rate and probability of death given encounter will exhibit a nonlinear relationship with total predation risk (Fig. 2d,f,j). A potentially fruitful avenue for future work will be to explore these nonlinearities to test whether or not inflection points in such relationships correspond to threshold values that trigger particular risk effects in prey. For example, some prey might respond only when a given risk cue (e.g., predator activity levels; Huang & Sih 1990) reaches a certain threshold while others might intensify antipredator behaviors continuously as such cues increase (Brown *et al*. 2006).

Uncertainties regarding subcategories' functional relationship to the components of predation risk notwithstanding, it is clear that subcategories capture different aspects of predation risk (Fig. 3). The majority of subcategories, and metrics therein, tend to capture variation in encounter rate rather than the probability of death given an encounter (Fig. 3). This is interesting given that many common risk effects observed in ungulates actually result in an *increase* in encounter probabilities. For example, ungulates have been shown to respond to risk by elevating vigilance rate (Laundré *et al.* 2001), forming larger aggregations (Moll *et al.* 2016a), and increasing use of open habitat (Valeix *et al.* 2009). Following Lima and Dill's (1990) definition of an encounter as the smaller distance of either species' detection radius, these three behaviors result in increased encounter rates by either increasing ungulates' ability to detect carnivores or making ungulates more conspicuous. Therefore, if such behaviors are to decrease overall risk over a given time period, they must substantially reduce the other major parameter in Eq. 1, the probability of death given an encounter (d). Indeed there is evidence that these behaviors reduce d: more vigilant ungulates are less likely to be attacked (FitzGibbon 1993), more open habitat can provide relative safety from ambush predators (Moll *et al*. 2016a), and larger group sizes dilute per capita risk (Dehn 1990). Conversely, behaviors explicitly aimed at avoiding encounters altogether, such as seasonal migrations, appear to be especially common when predator presence is spatiotemporally concentrated (i.e., predictably occurring in specific habitats or at specific times; Hebblewhite and Merrill 2007, Valeix *et al*. 2009, Thaker *et al*. 2011). These observations suggest the interesting possibility that when encounters are unpredictable or imminent, ungulates might mitigate risk using antipredator behavior that seeks to reduce death given an encounter, whereas if death given an encounter is probable but encounters are spatiotemporally predictable, ungulates might modify movement patterns, habitat use, or activity levels in an effort to reduce risk (Tollrian & Harvell 1998; Basille *et al.* 2015; Schmidt & Kuijper 2015).

Underlying this discussion is a broader issue relating to the spatial scales of predation risk and risk effects. Risky places metrics tend to represent risk at broader spatial scales, risky times metrics correspond to risk at finer scales, and habitat characteristics can span both. Similarly, the risk of encounter and the risk of death given an encounter tend to be related to broad and fine spatial scales, respectively. For example, elk can reduce encounter rates with wolves at the landscape and home range scales via migration and habitat selection, respectively (Hebblewhite & Merrill 2009; Bastille-Rousseau *et al.* 2015), while decreasing the probability of death given an encounter by elevating vigilance in fine-scale forage patches that are particularly dangerous (e.g., patches recently used by wolves or containing many fallen logs; Kuijper *et al*. 2014, 2015). Drawing on both terrestrial and marine literature, Wirsing and Ripple (2010) suggest that at the broadest scales, prey avoid encountering predators by changing habitat use, while at finer scales they decrease the probability of death given an encounter by using microhabitats that facilitate escape or by or being vigilant, a hypothesis consistent with what we have outlined above.

Perceived and actual risk

The variation revealed by our survey raises a question: are risk effects more related to actual predation risk (i.e., P(death) in Eq. 1) or risk as it is perceived by ungulates? The ability of prey to perceive risk and respond accordingly is foundational to risk effects theory, but we know strikingly little about this perception (Lima & Steury 2005). The assumption that prey have near-perfect information about true predation risk (i.e., P(death) in Eq. 1) is common in the risk effects literature (e.g., Luttbeg *et al.* 2003), but this notion has been largely untested (Lima & Steury 2005). Cresswell (2008) suggests that prey respond to perceived rather than actual risk, noting that experimental work demonstrates strong prey response to situations that seem risky, but are actually safe (e.g., experiments with impotent predators; Schmitz 2008). However, given that inducible antipredator behavior entails fitness costs (Tollrian and Harvell 1998, Creel and Christianson 2008), selection should oppose responses to impotent cues if they persist over long time periods. The notion that prey rely on simplified indices of risk supports the utility of using habitat characteristics to characterize risk, especially when cues emanating from predators are inconsistent or unreliable (Tollrian & Harvell 1998). A meta-analysis of the effect of risk on terrestrial species' foraging behavior found that habitat produced a stronger response than actual predators, although only two of the 31 studies included therein evaluated ungulates (Verdolin 2006). Studies that assess how well a given habitat characteristic correlates to true risk would enable evaluations of how ungulates trade-off efforts to assess true risk with the use of simpler indicators such as local habitat features.

RESEARCH RECOMMENDATIONS

Based upon our assessment and in the context of our framework, we offer the following recommendations for future carnivore-ungulate risk effects research:

1. Increase the diversity of carnivore species studied. The focus on gray wolves documented here stems from intense research effort surrounding wolf reintroduction into Yellowstone National Park. Much has been learned from this system, but there is danger of overgeneralizing the findings into other systems, such as those with more homogeneous habitat structure or different carnivore communities (see Schmidt and Kuijper 2015). There is an urgent need to assess risk effects from other carnivore species, especially species of conservation concern that have received little research attention (e.g., cheetah, tiger, snow leopard, and dhole). Increasing the diversity of carnivore species studied will also improve our limited understanding of how ungulates manage risk from multiple carnivores (Thaker *et al.* 2011).

2. Use established metrics when possible. We do not suggest any one subcategory of risk metric is "best", but several have more established precedence both in carnivore and non-carnivore systems, including predator density (Peacor & Werner 2001; Werner & Peacor 2003; Cresswell 2008), simulated chemo-olfactory cues (Weissburg *et al.* 2014) and "true" predation risk (i.e., P(death) in Eq. 1; Holling 1959, Lima and Dill 1990, Hebblewhite *et al*. 2005). Studies that model P(death) in Eq. 1 can also provide crucial ground-truthing context for understanding understand how well simpler, proxy-based metrics (i.e., habitat metrics) correlate to true risk. A minimal requirement for risk effects research should be a discussion of how the metrics in a given relates to studies using similar metrics (i.e., those in the same subcategory; Table 1). Novel or rarely-used metrics of risk might lead to important discoveries, but we suggest such metrics be carefully justified and compared to more established methodologies. Although the framework presented here is not intended to be normative, we hope it provides a starting place for a common language that can moves the field toward a more unified approach.

3. Use continuous rather than categorical metrics. Compared to continuous variables, nominal and ordinal variables tend to result in a loss of statistical and explanatory power (Caryl *et al.* 2014) and potentially increase the probability of Type I errors (Montgomery, Roloff & Ver Hoef 2011). Inference is particularly limited when presence/absence metrics are used because such metrics provide little mechanistic insight into ungulate behavior and omit important aspects of risk (e.g., predator density; Peacor and Werner 2001). Continuous metrics of predation risk will help move the field from an initial focus on merely documenting the presence of risk effects to an understanding of the their mechanics (Werner and Peacor 2003).

4. Choose metrics that enable testing of mechanistic hypotheses related to sensory cues of risk. We now recognize that risk effects are pervasive in carnivore-ungulate systems, but we know little about how ungulates perceive risk and which carnivore cues correspond to specific antipredator behaviors. Experimental studies that manipulated carnivore cues, including olfactory (e.g., urine), auditory (e.g., playbacks), and visual cues (e.g., visual models), in a variety of spatial concentrations over long periods (i.e., months or seasons) would provide insight into the immediate and long-term functional responses of antipredator behavior to threatening cues (Lima & Steury 2005; Cresswell 2008).

5. Appropriately interpret studies that employ a single risk metric. The growing body of ungulate risk effects research suggests that they are dynamic, scale- and species-dependent, and influenced by myriad environmental characteristics. Studies that employ a single risk metric likely only capture a snapshot into carnivore-ungulate dynamics. Such information is certainly useful, but we suggest inference resulting from such studies should be cautious and placed within the context of broader theory.

6. Test the risk allocation hypothesis while accounting for risk-related habitat characteristics. A recent synthesis suggests relatively broad support for the risk allocation hypothesis across taxa, provided study designs are of sufficient duration (Ferrari, Sih & Chivers 2009). The single study in our survey that explicitly tested the hypothesis in a wolf-elk system found strong support for it over the simpler risky places or risky times hypotheses (Creel *et al.* 2008). We suggest that the risk allocation hypothesis has the potential to unify the three broader categories of risk metrics presented here by placing ungulate response to risky times in a broader context of risky places and accounting for modulations of risk perception due to habitat characteristics.

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DATA ACCESSABILITY

The references for the literature survey and metrics contained therein are provided in supplementary material.

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FIGURE 1.

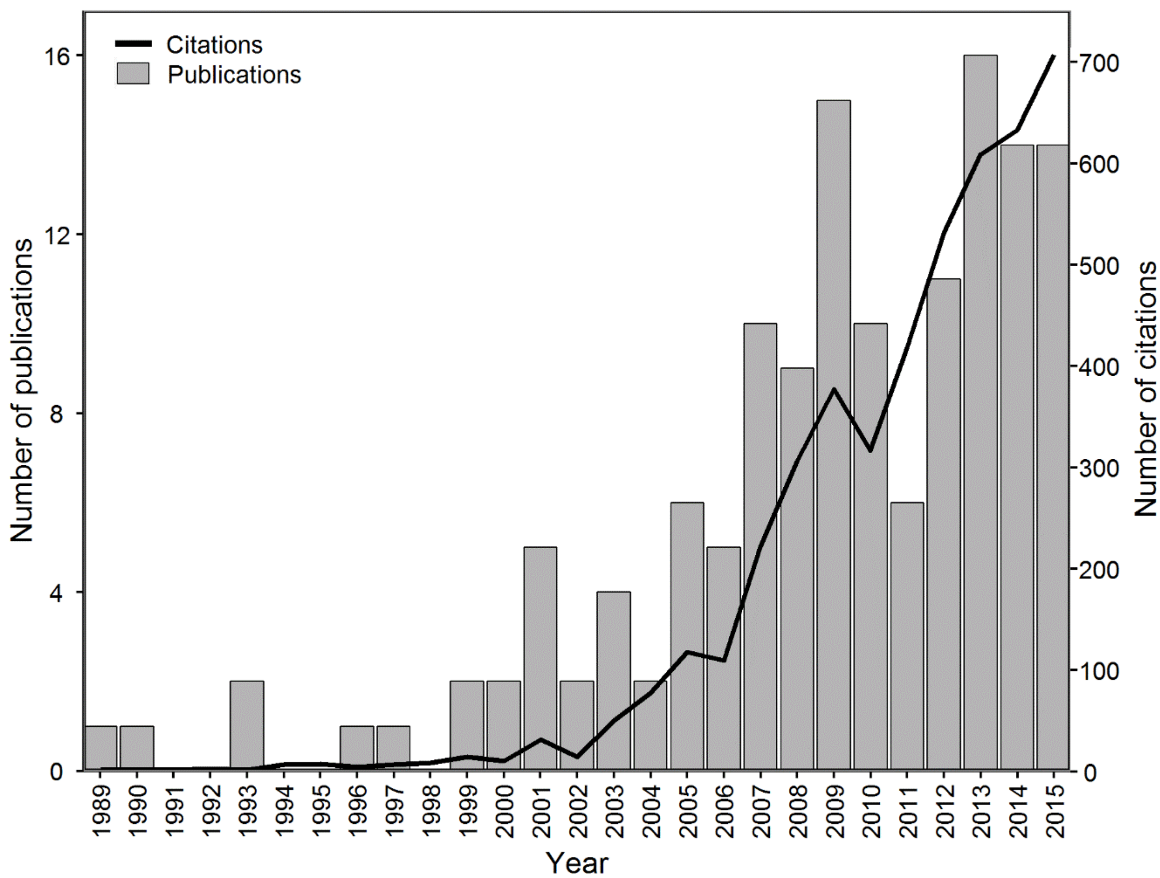


Figure 1. The number of carnivore-ungulate risk effects publications and associated citations by year as returned from a Web of Science literature search conducted in May 2016 (see text for search terms).

FIGURE 2.

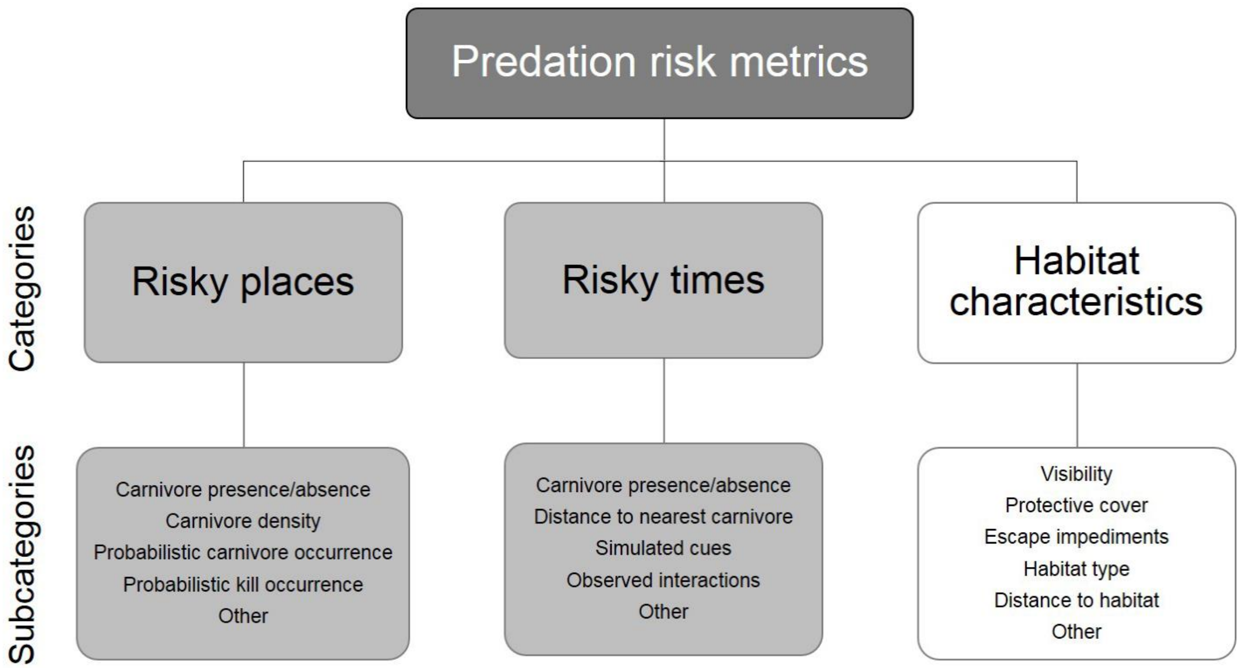
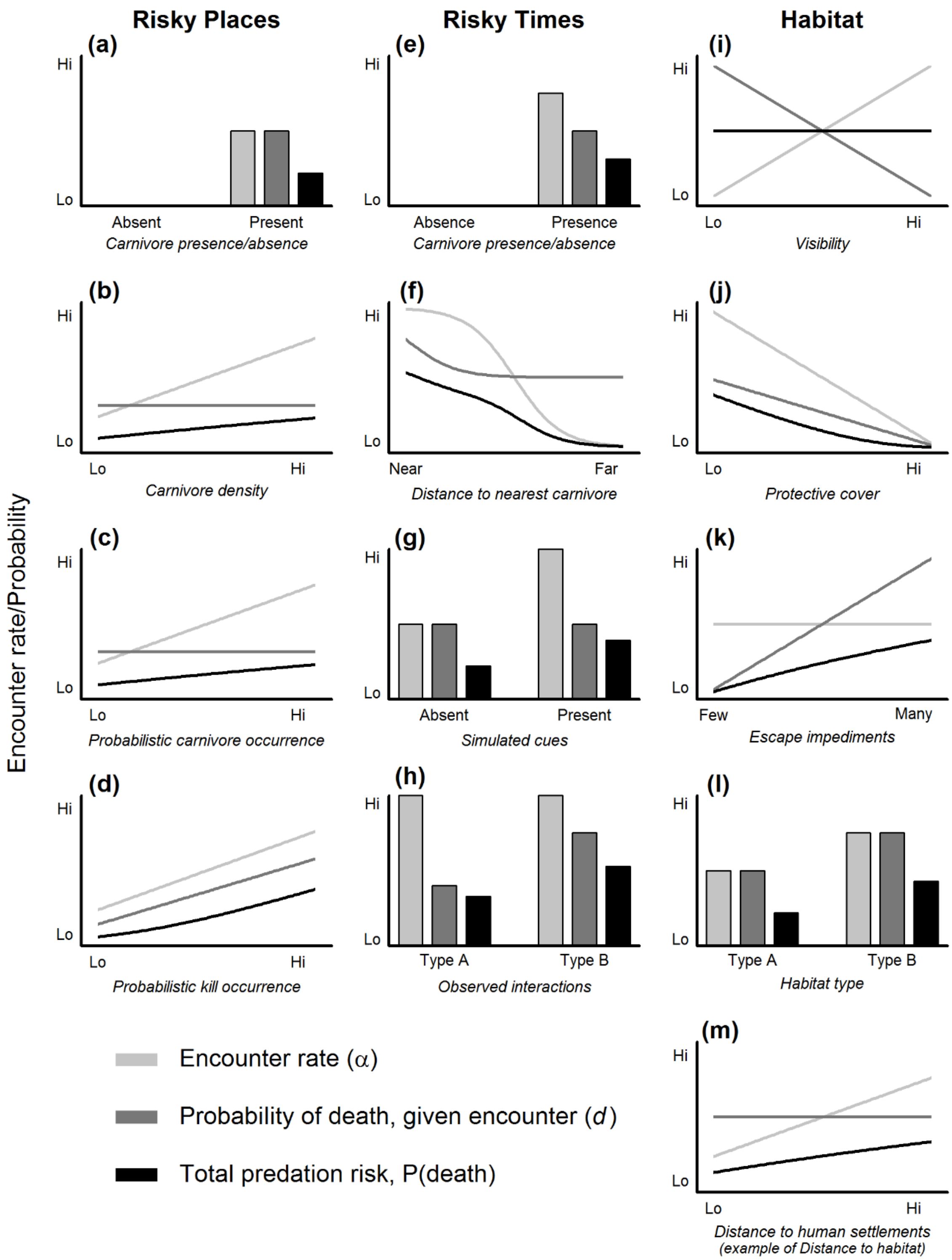


Figure 2. A framework for categorizing predation risk metrics, defined as a distinct characterization of predation risk within a given study. Light gray boxes are those which measure carnivore space use or behavior and white boxes are habitat-based.

FIGURE 3.



Risky Places
Risky Times
Habitat
(a)
Hi
Lo
Absent
Present
Carnivore presence/absence
(e)
Hi
Lo
Absence
Presence
Carnivore presence/absence
(i)
Hi
Lo
Lo
Hi
Visibility
(b)
Hi
Lo
Lo
Hi
Carnivore density
(f)
Hi
Lo
Near
Far
Distance to nearest carnivore
(j)
Hi
Lo
Lo
Hi
Protective cover
Encounter rate/Probability
(c)
Hi
Lo
Lo
Hi
Probabilistic carnivore occurrence
(g)
Hi
Lo
Absent
Present
Simulated cues
(k)
Hi
Lo
Few
Many
Escape impediments
(d)
Hi
Lo
Lo
Hi
Probabilistic kill occurrence
(h)
Hi
Lo
Type A
Type B
Observed interactions
(l)
Hi
Lo
Type A
Type B
Habitat type
Encounter rate (α)
Probability of death, given encounter (d)
Total predation risk, P(death)
(m)
Hi
Lo
Lo
Hi
Distance to human settlements
(example of Distance to habitat)

Figure 3. Hypothetical relationships between predation risk subcategories (see Table 2) and predator-prey encounter rates (light gray), probability of death given an encounter (dark grey), and total predation risk (black; see Eq. 1 in main text). Values and functions used are based upon Eq. 1 and reported rates for wolves and their ungulate prey (see Appendix C for details and code used to generate figures). Encounter rate in panel h represents simulated rather than true encounters.

Table 1. Descriptions and example references for subcategories of metrics characterizing predation risk from carnivores.

Category	Subcategory	Description and example references
Risky places	Carnivore presence/absence	Presence and absence of carnivores captured spatially (e.g., areas with and without carnivores; Laundré *et al*. 2001) or temporally (e.g., pre- and post-colonization; Christianson and Creel 2014)
	Carnivore density	Carnivore densities (White *et al*. 2009) or carnivore-to-ungulate ratios (Creel *et al*. 2007)
	Probabilistic carnivore occurrence	Two common forms: 1) occurrence modeled probabilistically using locational data (e.g., GPS-collars) and kernel-based techniques (Thaker *et al.* 2011), or 2) resource selection functions that couple locational data and habitat characteristics (Bastille-Rousseau *et al*. 2015)
	Probabilistic kill occurrence	Models predicting where kills are likely to occur, usually built as a function of habitat features and/or probabilistic models of carnivore occurrence (Hebblewhite and Merrill 2007)
Risky times	Carnivore presence/absence	Local presence and absence of carnivores during a short time frame (e.g., a 24-hour period; Creel *et al*. 2005)
	Distance to nearest carnivore	Instantaneous distance between an ungulate and a carnivore measured via location data (e.g., both individuals wearing GPS-collars; Middleton *et al*. 2013)

	Simulated cues	Olfactory (e.g., scat; Kuijper *et al*. 2014) or auditory (e.g., playback calls; Dalerum and Belton 2015) cues that mimic immediate carnivore presence or recent past presence
	Observed interactions	Real-time observations of carnivore-ungulate interactions (Lingle 2002)
Habitat characteristics	Visibility	Any metric indexing visibility, including topography (Acebes *et al*. 2013), vegetation density (Riginos 2015), and scores derived from obscurity boards or straight-line distances to obstructions (Ripple and Beschta 2006)
	Protective cover	Habitat characteristics expected to decrease risk by providing concealment (e.g., dense vegetation) or acting as predator refugia (e.g., steep slopes; Corti and Shackleton 2002)
	Escape impediments	Presence and/or density of obstructions (e.g., logs, boulders) that inhibit an ungulate’s flight (Kuijper *et al.* 2015; Painter *et al.* 2015)
	Habitat type	Habitats deemed risky (e.g., edge habitat; Altendorf *et al*. 2001) or safe (e.g., open habitat; Marino 2012).
	Distance to habitat	Distance between ungulates and a habitat type (e.g., wolf-occupied forest; Hayward *et al*. 2015) or habitat feature (e.g., human settlement; Kuijper *et al*. 2015)

TABLE 2. Distribution of metrics used to characterize predation risk into categories and subcategories of risk (see text). Metrics were extracted from a survey of the carnivore-ungulate risk effects literature conducted May 2016.

Category	Subcategory	No. studies	% studies	No. metrics	% metrics
Risky places	Carnivore presence/absence	28	19.%	28	11.5%
	Carnivore density	16	11.3%	17	7.0%
	Probabilistic carnivore occurrence	24	17.0%	37	15.2%
	Probabilistic kill occurrence	15	10.6%	20	8.2%
	Other	11	7.8%	11	4.5%
	Total	78	55.3%	113	46.5%
Risky times	Carnivore presence/absence	19	13.5%	21	8.6 %
	Distance to nearest carnivore	8	6.4%	10	4.1%
	Simulated cues	12	8.5%	17	7.0%
	Observed interactions	5	3.5%	5	2.1%
	Other	3	2.1%	4	1.6%
	Total	45	31.9%	57	23.5%
Habitat characteristics	Visibility	13*	9.2%	22*	9.1%
	Protective cover	9	6.4%	16	6.6%
	Escape impediments	10*	7.1%	12*	5.0%
	Habitat type	10	7.1%	10	4.1%
	Distance to habitat	8	5.7%	10	4.1%

	Other	2	1.4%	5	2.1%
	Total	34	24.1%	73	30.0%

*Two studies contained a metric that combined escape impediments and visibility into one variable; this metric was therefore included in both subcategories.

AUTHOR CONTRIBUTIONS

RJM led the project. RJM, KMR, TM, ABM, SMG, and LA conducted the literature survey and produced figures and tables. All authors contributed substantially to the manuscript’s conception, development, writing, and revision.